Reference: *Biol. Bull.* 157: 445–452. (December, 1979)

PARTHENOGENESIS IN *COPTOPTERYX VIRIDIS*, GIGLIO TOS (1915) (DYCTIOPTERA, MANTIDAE)

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The mantid *Coptoteryx viridis* has been studied for several years in our laboratory. As its behavior is similar to that of other species of the sub-order Mantodea, we considered the possible existence of a parthenogenetic reproduction mechanism. These animals are solitary and sedentary, and the female often kills the male before copulation takes place. The average adult life of the female is twice as long as that of the male (Guerrero, Maggese and Cukier, 1977).

Observations made by other workers indicate that *Brunneria borealis* reproduces exclusively by parthenogenesis (White, 1948a) and *Miomantis savignii* (Adair, 1925) reproduces both by parthenogenesis and by being fertilized. The present investigation was designed to determine the existence and type of parthenogenesis in *C. viridis*.

Materials and Methods

Oothecas of *Coptoteryx viridis* were gathered in the vicinity of the slaughterhouse of Lisandro de la Torre in Buenos Aires city, and were kept in separate flasks. The nymphs which emerged from these oothecas were kept in individual cages for their whole life, at room light and temperature. The cages and the method of feeding were as described by Guerrero and De Carlo (1976).

Male nymphs of the 5th and 6th nymphal stages were employed for determination of the karyotype, and females of the 7th nymphal stage were used to corroborate the results. The testes and ovaries were immersed in an hypotonic solution of 0.7% Na citrate, fixed in Carnoy and stained with Giemsa.

Levan's classification was used to determine the karyogram where the centromeric index is $Ic = 100\ s/c$ where s is short arm and c is whole length. Chromosomes with values of the index (Ic) of 50 are termed metacentric (type M); of from 50 to 37.5, metacentric (type m); 37.5 to 25, submetacentric (type Sm); 25 to 12.5, subelocentric (type st); 12.5 to 0, acrocentric (type t); and of 0 are termed telocentric (type T).

Study of the embryos involved fixation in Bouin, followed by manual elimination of the chorion, embedding in parafin, sectioning at 7 μ thickness, and staining with hematoxylin-eosin.

Results

Seven of the 13 females which arrived at the adult stage laid oothecas without fertilization. The number of oothecas laid by a female varied from 1 to 7, the variation depending on the time they lived as adults and on the time of the year in which they attained adulthood.

TABLE I

Animal No.	Date of birth	Date of molting to imago	Total nymphal life (days)	Time between the arrival to the adult stage and the first laying (days)	Number of oothecas per female	Interval between layings (days)	Total life time (days)	Date of death	Date of the last laying	Time between the last laying and death (days)
I(17)	22-Sep-75	26-Dec-75	95	80	2	9	203 108	12-Apr-76	24-Mar-76	19
IX(1)	15-Sep-75	22-Dec-75	98	77	1	—	178 80	11-Mar-76	8-Mar-76	3
X(3)	26-Sep-75	26-Dec-75	91	62	7	14 6 14 8 11 11	217 126	30-Apr-76	30-Apr-76	0
X(19)	3-Oct-75	26-Dec-75	84	77	3	19 7	199 115	19-Apr-76	7-Apr-76	12
X(22)	6-Oct-75	16-Jan-76	102	59	6	8 15 12 15 13	231 129	24-May-76	17-May-76	7
X(30)	13-Oct-75	19-Jan-76	98	69	1	—	167 69	29-Mar-76	29-Mar-76	0
X(37)	22-Oct-75	8-Mar-76	137	—	—	—	152 15	23-Mar-76	—	—
XII(82)	13-Oct-75	2-Mar-76	137	30	4	11 7 14	205 168	15-Aug-76	3-May-76	106

A total of 22 oothecas was laid by the 7 females (Table I). The time that elapsed between the achievement of the adult stage and the laying of the first ootheca varied from 30 to 80 days. The female that had laid her first ootheca on the 30th day had become an adult towards the end of the summer (2-Mar-76), whereas the one that delayed 80 days in laying her first ootheca had attained adulthood at the beginning of the summer (26-Dec-75). The rest of the females laid their first ootheca towards the end of the summer, having attained the adult stage at the beginning of that season. In general, the sooner they became adults the longer they delayed in laying their first ootheca.

The first ootheca was laid on 26-Feb-76 and the last one on 4-May-76, a span of two and a half months. The intervals of time between one laying and the next for all the females was from 6 to 19 days. The average intervals between successive layings per female varied between 9 and 13 days and the general average of intervals for all the oothecas laid by the 7 females was 11 days.

As a rule the females died immediately after their last laying, or a few days after it. The exception was one female (XII-82) which had arrived at the adult stage at the end of the summer, and lived 106 days after her last laying. As this laying took place at the beginning of May, it might be asked whether cessation of laying was due to low temperature, photoperiod or any other reason. Her ovaries were full of mature eggs.

The female IX-I died 3 days after laying her last ootheca, with her ovaries full of mature eggs. They were not vestigial eggs since the last ootheca laid was of an enormous size. The female X-22 died 7 days after her last laying, and she had her ovaries full of mature eggs. The female X-30 laid her last ootheca on the day of her death, and her ovaries had no mature eggs. The female X-37 lived 15 days of adult life and her ovaries were full of mature eggs. She did not lay oothecas.

According to the present observations (Table I) it seems that the female would need a stimulus to start laying oothecas. This stimulus could be the presence of a male, if there was one; otherwise the female would wait until the last moment to lay her oothecas. Other probable stimuli could be environmental factors such as temperature and photoperiod. Once the process of laying started, it would not cease until the female died, or the environmental conditions turned unfavorable. It seems that the laying would depend on a certain period of the year more than on the chronotropic age of the individual. These data also indicate that about 30 days are needed to begin laying and that the yolk replacement is significant.

The next step was to wait until the oothecas hatched, since we were not sure that they contained viable eggs. The first nymph hatched 6 months and 18 days after laying, on 11-Oct-76 (Table II) and the last one on the 15-Jan-77.

According to our data for non-parthenogenetic populations, hatching never occurs after this date (Guerrero, Maggese, Cukier, 1977). The average interval between the laying of the ootheca and the first hatching was 7.5 months. From the 22 oothecas laid, 9 hatched nymphs, and 8 of the remaining 13 oothecas exhibited exposed cells that caused the eggs to dry. The number of nymphs ecloded per ootheca was very low, between 1 and 5. A total of 23 nymphs were hatched.

TABLE II

Individual N	Ootheca N	Number of hatched nymphs	Sex	Date of laying	Date of the first hatching	Time between laying and hatching	Date of the last hatched nymphs
X-22	1	2	female	15-Mar-76	3-Nov-76	7 months and 19 days	13-Dec-76
X-3	1	4	female	17-Mar-76	22-Nov-76	8 months and 8 days	25-Nov-76
X-22	2	3	female	23-Mar-76	11-Oct-76	6 months and 18 days	15-Jan-77
1–17	1	5	female	24-Mar-76	17-Nov-76	7 months and 24 days	13-Dec-76
X-3	2	1	female	31-Mar-76	7-Dec-76	8 months and 7 days	7-Dec-76
X-19	1	2	female	31-Mar-76	29-Nov-76	8 months	7-Dec-76
XII-82	1	1	female	3-May-76	29-Dec-76	7 months and 24 days	29-Dec-76
X-19	2	1	female	7-Apr-76	6-Dec-76	8 months	6-Dec-76
X-22	3	4	female	15-Apr-76	22-Oct-76	6 months and 3 days	13-Dec-76

The nymphs were all females, with a highly restricted viability since none of them passed the second nymphal stage (they lived between 0 and 14 days). Due to these results, the oothecas were kept for observation.

At the beginning of May, some of the parthenogenetic oothecas were opened and eggs in perfect state were found inside them. These eggs were fixed, embedded in paraffin and stained, revealing a very early stage of development. They presented a blastoderm along the surface with a ventral thickening that would represent the beginning of the development of the germinal band.

Oothecas collected from nature after the hatching period (3 months) also contained fresh eggs in the same stage of development. In these last oothecas it was found that several of those that had yielded a low progeny had a great number of empty chorions.

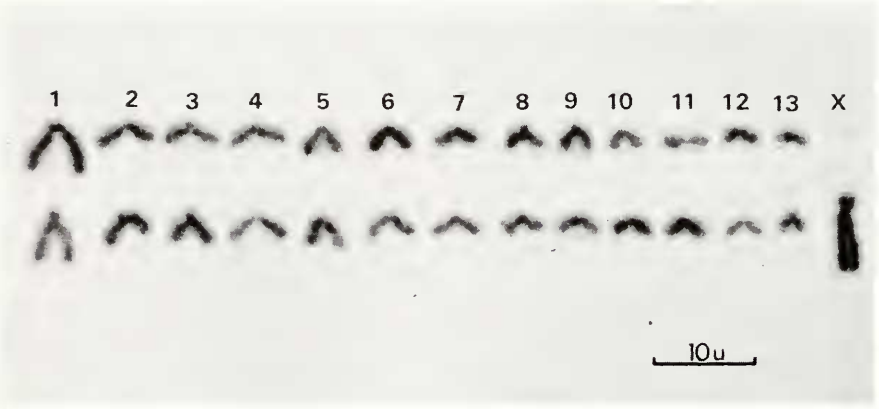

FIGURE 1. Diploid karyogram of *Coptoptcryx viridis*. This was made from two metaphases of the second meiotic division.

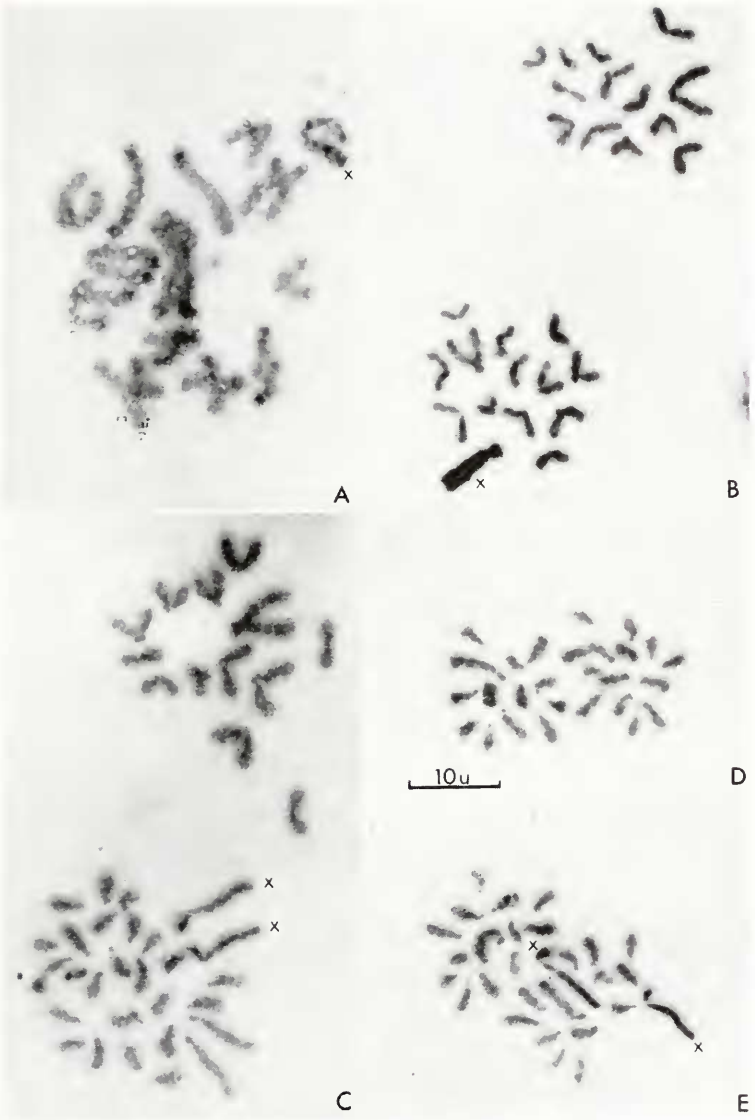

FIGURE 2. Chromosomes of *Coptopteryx viridis*. A) Diakinesis. B) two metaphases of the second meiotic division (with 13 and 13-X chromosomes). C). A metaphase of the second meiotic division with 13 chromosomes and an anaphase with 28 chromosomes. D) Telophase with 13 and 13 chromosomes. E) Telophase with 13 and 13-X chromosomes.

This evidence gave rise to two possibilities: either the existence of an annual-biennial cycle gave rise to two types of eggs, some with a slower development than others, or the development of the eggs after a certain stage had ceased for some reason (the structure of the ootheca would have allowed them to remain fresh). Kume and Dan (1968) observed in *Paratenodera aridifolia* that in the diapause

coincident with hibernation the embryos were in the same stage of development as ours.

It was decided to wait until the next spring to see which of the two alternatives was correct. The first proved to be valid, since on 22-Nov-77 nymphs started hatching from the parthenogenetic oothecas laid during the Summer-Autumn period of 1976 and which had already hatched nymphs in the Spring-Summer of 1976–1977; nevertheless the birth frequency was very low.

The next step was to determine the karyotype of the non-parthenogenetic individuals of this species. It was found that the male has 13 autosomes and a sexual chromosome as haploid number. Figure 1 shows the diploid karyogram of the species. It can be seen that it has acrocentric autosomes of the "t" type according to the classification of Levan, Fredga and Sandberg (1964), and the X chromosomes is subtelocentric of the "st" type according to the same classification.

This karyogram was built from two metaphases of the second meiotic division, with 13 and 13-X chromosomes respectively. As can be seen in the diakinesis of Figure 2a and in many others observed in this study, no trivalent chromosomes were found, which led us to the conclusion that this species belongs to the XX system for the female and XO for the male. Figure 2b shows two metaphases of the second meiotic division, with 13 and 13-X chromosomes respectively.

Figure 2c shows a metaphase of the second meiotic division with 13 chromosomes and an anaphase with 28 chromosomes which is the result of the separation of chromatids from the metaphase of the previous figure (2b). Figure 2d and 2e show two telophases, one with 13 and 13 chromosomes and the other with 13 and 13-X chromosomes respectively, indicating the end of the meiosis seen in figure 2c. All of these, and other figures studied, made us think that this species belongs to the type XX-XO with a diploid number of 27 chromosomes for the male and 28 for the female.

Discussion

The only species studied with this type of reproduction has been *Brunneria borealis,* from Central Texas and North Carolina, which reproduces exclusively by parthenogenesis (White, 1948) and *Miomantis savignii* (Adair, 1925) from Egypt, which reproduces both by parthenogenesis and after fertilization.

It has been seen in *Coptopteryx viridis,* that the beginning of oviposition varies within a very wide range and is related to the moment in which the animals attain the adult stage. This laying would be related to a certain period of the year more than to the age of the individual. This might explain why the female that reached the adult stage at the beginning of summer delayed 80 days in laying her first ootheca, whereas the one attaining maturity at the end of the same season took 30 days in doing so (Table I). From the analysis of the ovaries studied it is not clear whether or not the growth of the oocytes is synchronous with the process of nuclear maturation (meiosis).

The study of the oogenesis of this species will help to clarify this point. It was observed that the chromosome morphology of *Coptopteryx viridis* differs from that of other species of mantids described by White (1941) and Hughes-

Schrader (1943). These authors studied species from Europe, Africa and Central and North America and found that in most of them the autosomes are metacentric or "M" type, according to the classification of Levan (1964), with some of the submetacentric or "sm" type, according to the same classification. Nevertheless, the sexual chromosomes have the same configuration. This shows a marked difference with the chromosomes of *Coptopteryx viridis* where the autosomes are acrocentric or of the "t" type and the X chromosome is subtelocentric or of the "st" type according to Levan (1964). These data suggest that this is a diploid parthenogenesis, since haploid parthenogenesis never yields females. From this point, two possibilities arise: that the parthenogenesis is automictic or apomictic. In the first case the parthenogenesis would be exclusively thelytoky because of the sexual configuration of the species. In the second case, and due to the low number of hatched nymphs, it could be a thelytoky or amphitoky parthenogenesis. This last type of parthenogenesis would yield males by abnormal meiosis, as occurs with the Aphides (Homoptera) which have a XX-XO sexual system (Lees, 1961). This did not occur in *Coptopteryx viridis,* therefore we are inclined to think that this is a case of diploid parthenogenesis, automictic or apomictic, but exclusively thelytoky. Nevertheless, due to the low viability of the indviduals, it is possibly an automictic parthenogenesis, since homocygosis favors the expression of deletereous genes.

The authors express thanks to Dr. C. Naranjo for photographic assistance.

Summary

Several years of observations of the behavior of the mantid *Coptoteryx viridis* suggested evidence of parthenogenesis in this species. *C. viridis* is a solitary, sedentary animal, where the female often kills the male before copulation takes place, and the average male adult life is half that of the female.

Virgin females were reared in our laboratory from their hatching to the end of their lives; these laid oothecas. From these oothecas, parthenogenetic nymphs were born, all of the female sex and with a very low viability. The karyotype of the non-parthenogenetic individuals of this species was found to be XO-XX with a diploid number of 27 chromosomes for the male and 28 for the female. The autosomes were acrocentric or "t" type while the X chromosome was subtelocentric or "st" type, according to Levan's classification.

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